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Research article

Disentangling the effects of temperature and rainfall on the population dynamics of Kalahari meerkats

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In arid habitats, recent increases in summer temperatures associated with global warming are adversely affecting many animal populations. However, annual rainfall also varies widely in many of these areas, and we do not yet fully understand the relative impact of variation in temperature and rainfall on the demography of arid-zone species. Here, we examine the effects of temperature and rainfall variation on the demography of meerkats *Suricata suricatta* in the southern Kalahari over the last 25 years. During this period, average maximum monthly air temperatures at our study site increased by around 1.5°C to 3.2°C, while annual rainfall fluctuated without a consistent trend. We show that annual changes in female fecundity and recruitment were more closely correlated with variation in rainfall. Increasing air temperatures were associated with reductions in the recruitment of pups and the survival of some age classes but, in most cases, the demographic consequences of high temperatures were modest compared to the effects of low rainfall, which in some years led to the near cessation of successful reproduction and the extinction of many smaller groups. For instance, exceptionally low rainfall in 2012–2013 was associated with low recruitment and with declines in group size and population density, which fell by over 50%. Unusually hot years did not have similar consequences. Following the 2012–2013 drought, intermittent years of low rainfall and frequent droughts continued to suppress recruitment and slowed the population's recovery. Future changes in temperature may affect the dynamics and size of the meerkat population, but our work suggests that over the last 25 years, annual changes in rainfall have exerted a stronger influence on meerkat demography. Our study demonstrates the importance of long-term, individual-based data for determining how changes in climate affect the dynamics of animal populations, especially in arid environments where bottom-up processes often dominate.

Keywords: climate change, cooperative breeding, drylands, droughts, global heating, population dynamics



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Introduction

Global temperatures have been rising steadily over the last century (IPCC 2022), with some of the strongest warming occurring in arid regions (Kruger and Sekele 2013, Zhou et al. 2015). High temperatures in these areas have been associated with declines in the reproductive output and survival of numerous animals, and there is a growing consensus among scientists that global warming is impacting arid-zone populations (Cruz-McDonnell and Wolf 2016, Iknayan and Beissinger 2018, Ridley et al. 2021, Fuller et al. 2021). For example, in birds living in the arid savannas of the southern Kalahari and in the deserts of Australia, recent high temperatures have been linked to cumulative body mass loss (du Plessis et al. 2012, Gardner et al. 2016, van de Ven et al. 2019, Kemp et al. 2020), reduced nestling growth rates (Cunningham et al. 2013), and increased breeding failure (D'Amelio et al. 2021, McCowan and Griffith 2021, Pattinson et al. 2022), leading to alarming forecasts for some bird communities in the coming decades (Conradie et al. 2019, Ma et al. 2023, Payne et al. 2023). Though less frequently documented, mounting evidence suggests that rising temperatures in arid areas are also having detrimental effects on mammal populations (Welbergen et al. 2008, Moses et al. 2012, Woodroffe et al. 2017, Fuller et al. 2021).

Global warming has drawn attention to the effects of temperature on arid-zone species, but the defining characteristic of these regions – which cover some 27.3% of the world's land surface (Wang et al. 2022) – is their low and unpredictable rainfall (Ward 2016, Lovegrove 2021). Consequently, the life histories of most arid-dwelling animals are shaped by the availability of water and its influence on food resources (Louw and Seeley 1982, Lovegrove 2021). Supporting this view, demographic studies of mammals have commonly identified rainfall as the key regulator of their population dynamics (Dickman et al. 1999, Brown and Ernest 2002, Bateman et al. 2011, Greenville et al. 2012, Barros et al. 2018). Episodic rainfall patterns are known to drive the irruptive cycles of many desert rodents (Brown and Ernest 2002, Holmgren et al. 2006, Greenville et al. 2012, 2013), and prolonged drought conditions have been shown to cause large population crashes in ungulates, particularly in non-migratory populations (Ogutu et al. 2008, Smit et al. 2020, Taggart et al. 2020, Owen-Smith 2021). Similar patterns have been observed in other taxa. For example, a series of major droughts in Australia in the 1970s and 1980s brought about steep declines in several marsupial populations (Caughley et al. 1985, Gordon et al. 1988). And in the Kalahari Desert, the placement of body temperature loggers in aardvarks *Oryzomys afer* during a drought revealed a steady decline in body condition that ended in starvation for many individuals (Rey et al. 2017).

The wildlife of arid regions has long adapted to the boom-bust conditions of their environment, persisting at low numbers during the most stressful periods and rebounding when conditions are more favourable. However, there are concerns

that ongoing climatic changes will alter the severity and frequency of these fluctuations and that this will threaten the viability of many populations, particularly if environmental changes occur alongside other pressures (Smit et al. 2020, Dickman and Pavey 2023, Zhang et al. 2023).

Predicting how a given population will respond to environmental change is further complicated by the fact that, while herbivore and insectivore numbers are often strongly regulated by rainfall patterns, top-down effects, such as predation, also play a significant role in many systems (Owen-Smith and Mills 2006, Letnic and Crowther 2012, Greenville et al. 2017). With responses to environmental change also likely to vary across trophic levels (Mills 1995, Greenville et al. 2014, Prugh et al. 2018), and to depend upon species-specific aspects of physiology and behaviour, there is an urgent need for more demographic studies in arid environments. Such information is important not only for advancing academic understanding but also for prioritising conservation efforts and guiding decisions about how natural resources are managed (Lewin et al. 2024).

To date, demographic studies of mammals that can draw on detailed records of the life histories of individuals come primarily from populations living in mesic, temperate areas (Salguero-Gómez et al. 2016), and similar information is available for comparatively few populations in arid or semi-arid areas (Nater et al. 2018, Rabaiotti et al. 2023, Thorley et al. 2023). As a result, the extent to which different environmental factors affect specific vital rates have seldom been quantified, and the relative contributions of reproduction and survival to mammalian population dynamics is often unknown. Moreover, many mammals living in arid environments are social and live in structured groups, the size and composition of which can have strong effects on population dynamics through both within- and between-group processes (Dyble et al. 2019, Rabaiotti et al. 2023, Lerch and Abbott 2024). As environmental factors have the potential to alter and interact with the size and structure of social groups (Groenewoud and Clutton-Brock 2021, D'Amelio et al. 2021, Bourne et al. 2023), social effects need to be considered when evaluating the vulnerability of many arid populations to climate change.

In this paper, we explore the effects of changes in rainfall and temperature on the demography and dynamics of a population of meerkats *Suricata suricatta* in the southern Kalahari, using 25 years of data on the reproductive performance and survival of large numbers of individuals and groups. As singular cooperative breeders, meerkat groups are stable and successful reproduction is skewed towards a single dominant female who produces up to four litters of 2–7 pups per year, typically fathered by the most dominant immigrant male in her group (Clutton-Brock and Manser 2016). Other group members of both sexes help to feed and protect the offspring of the dominant female (Clutton-Brock et al. 2001a). Older subordinate females occasionally attempt to breed, though their success in recruiting pups is lower than that of dominant females, who commonly kill litters born to other

females and evict their mothers (Clutton-Brock and Manser 2016).

Earlier studies of meerkats in the Kgalagadi Transfrontier Park – formerly the Kalahari Gemsbok Park – found that interannual variation in rainfall caused substantial fluctuations in the population's size (Doolan and MacDonald 1997, Clutton-Brock et al. 1999a). Annual mortality of meerkats was high in all years and did not vary consistently with rainfall, but groups that failed to breed declined rapidly (Clutton-Brock et al. 1999b). Following the drought of 1994/1995, multiple groups went extinct, and the overall population size decreased by around 70% (Clutton-Brock et al. 1999a).

Here, we investigate how climatic factors have affected the dynamics of a separate meerkat population located 150 km to the east of the Kgalagadi Park at the Kuruman River Reserve. Predators at our study site are common though less abundant than in the Park, resulting in lower adult mortality rates (Clutton-Brock et al. 1999b). Previous research has shown that, similar to the Park, group sizes and population density at the Reserve respond positively to rainfall (Bateman et al. 2011, 2013, Ozgul et al. 2014). Increased rainfall has also been linked to higher body weights, more frequent breeding in adult females, and greater pup survival (Groenewoud and Clutton-Brock 2021), while high summer temperatures have been shown to reduce the daily weight gain, growth and survival of pups (van de Ven et al. 2020). In contrast, rising winter temperatures have been associated with increased adult body weight and higher adult survival at the start of the breeding season (Paniw et al. 2019). Warmer temperatures year-round may also increase the incidence of tuberculosis, which has the potential to destabilise groups and increase their probability of extinction (Paniw et al. 2022). However, despite the progress made by this previous work, a broader comparison of the importance of rainfall versus temperature on specific demographic components has not yet been undertaken.

We begin by describing the long-term changes in rainfall and temperature at our study site, within and between years. We then explore the relationship between rainfall and NDVI (normalised difference vegetation index), a measure of primary vegetation productivity likely to be correlated with the abundance of invertebrate herbivores, which form the main part of the meerkat's diet (Doolan and MacDonald 1996). Next, we detail the long-term changes in population density, mean group size and various demographic parameters that have taken place in the meerkat population. Finally, we examine the effects of variation in temperature and rainfall on the reproductive output of groups, the survival of different age classes, and on overall changes in group size and population density. To increase our confidence in the climate-demography relationships we report, we include analyses of detrended time series to determine whether these relationships could be separated from longer term trends in climate, or other correlated, but unmeasured variables (Cruz-McDonnell and Wolf 2015, Iler et al. 2017).

Material and methods

Study population and demographic data

An individual-based study of meerkats has been running at the Kuruman River Reserve in South Africa since 1993 (26°58'S, 21°49'E, Clutton-Brock and Manser 2016). The study area, which covers approximately 50–60 km², includes a diverse landscape of dry pans, vegetated sand dunes, and arid bushveld that is typical of a South African savannah, where livestock and game farming form the principal land use. Since the start of the project, approximately 15 groups (range = 6 to 21 groups) and around 200 individuals were followed at any one time (mean ± SD per month = 214.5 ± 59.4, range = 101 to 359). Most individuals were born into the study population and were habituated from birth to allow close behavioural observation. Groups were visited 3–4 times per week in the morning and afternoon throughout the study, with data collected on the composition of groups and on the behaviour, reproductive status, social status, and health status of individuals, so that pregnancies, births, deaths, emigrations and immigrations could be enumerated (summarised in Clutton-Brock and Manser 2016). Most individuals in the population were also weighed at each visit by enticing them onto electronic scales with small amounts of hard-boiled egg or water, and while foraging. GPS locations were taken from the center of the group at 15 min intervals, which we use to estimate home ranges. Though the project began in 1993, all the above data were only collected on multiple groups (> 5) simultaneously from 1998 onwards. Most of our analyses therefore cover the breeding seasons from 1998–2023. The only exception is the GPS data, which were collected in the form needed for our analyses from 2002 onwards. Analyses that make use of population density, which is derived from these GPS data, therefore span 2002–2023. As rainfall in the Kalahari is restricted to the austral summer, we defined each year as starting midway through winter, on 1 July.

Using the life-history data we compiled a monthly census of all groups in the population. In many cases the deaths and emigrations of individuals were known, but when the fate of individuals was unclear, we relied on behavioural data to inform our decision (Bateman et al. 2011, Ozgul et al. 2014). From the census, we quantified annual demographic parameters for each group: 1) the number of times the dominant and subordinate females fell pregnant (fertility), 2) the number of litters born to dominant or subordinate females (fecundity), 3) the number of emergent pups, 4) the number of recruited pups (recruitment), 5) pup survival, and 6) non-pup survival. Recruitment and pup survival were considered to nutritional independence at 90 days. For reproductive measures, we included groups that persisted from one season to the next, while for survival measures all groups with an established dominant female at the start of the year were included.

To investigate the effect of climatic variables on population dynamics, we used population density as an index of population size. Population density is highly correlated

with the mean group size (Pearson's $r=0.81$, $df=257$, $p < 0.001$). To calculate population density, we first estimated the home ranges of all established groups in rolling three-month windows (Jul–Sep, Aug–Oct, etc.). Meerkat home ranges are relatively stable and GPS data collected over three months is sufficient to estimate home ranges in our population accurately (Kranstauber et al. 2019). Based on our own sensitivity analyses (Supporting information), we included the home ranges of groups that had been visited at least 20 times across a three-month window (mean \pm SD = 56.1 ± 19.0 visits, range = 20 to 119). Home ranges were estimated as the 95% kernel density estimate (KDE) of all foraging locations ('ctmm' R package: www.r-project.org, Fleming and Calabrese 2022). We merged the 95% KDE home ranges of groups to give the 'total population area' in each window. Population density was calculated as the meantotal number of individuals in all groups, divided by the total population area. Similarly, group density was the number of groups divided by the total population area.

Climate data

Climate data included both site-measured and remotely sensed variables. We obtained daily maximum near-surface air temperatures (2 meters) for our field site from the Climate Prediction Center's (CPC) global temperature product (NOAA 2023a). These data are provided on a 0.5-degree longitude-latitude grid and are strongly correlated with analogous measurements made by a weather station located at the centre of the study area (Pearson's $r=0.987$ [95%CI: 0.983, 0.990], Supporting information). As the weather station started recording in 2010, we used CPC temperature data to cover the span of our study. We averaged the daily maximum temperature according to the needs of each analysis: by month when modelling long-term seasonal variation in temperature, and over specific periods of the year for demographic analyses, corresponding to ecologically relevant windows.

Rainfall has been measured consistently at our field site since 1998. Before 2010, manual recordings were made using a rain gauge, while from 2010 onwards, rainfall was recorded by a weather station. Despite combining two methods of data collection, rainfall taken from this combined dataset displayed a stronger correlation with annual vegetation productivity at our field site than rainfall data taken from the CPC product (NOAA 2023b) or from the Global Precipitation Climatology Project ver. 3.2 (GPCP, Huffman et al. 2023), two prominent remotely sensed datasets (Supporting information). We therefore used site-measured rainfall to describe variation in rainfall across the span of our study, and for demographic analyses, and the GPCP data to characterise long-term rainfall trends.

To evaluate how changes in air temperature and rainfall have contributed to changes in the relative dryness of the Kalahari at our study site, we extracted the standardised precipitation index (SPEI) from the global SPEI database (Beguería et al. 2014). We focussed on SPEI at a 6-month

scale to capture the short-term effects of water load on plant growth and more delayed effects on insect herbivores. Since the global SPEI data are based on remotely sensed rainfall estimates, we also calculated SPEI using site-measured rainfall data with the 'SPEI' R package (www.r-project.org, Beguería and Vicente-Serrano 2017). Although the site-measured data covers a shorter period, it provides a more accurate measure for our study and was therefore used in demographic analyses. Potential evapotranspiration in the SPEI calculation was estimated using Hargreave's formula and CPC temperature data.

Vegetation productivity

We estimated the vegetation productivity of each growing season in each year using NDVI (normalised difference vegetation index) values taken from the MODIS MOD13Q1 product (Didan et al. 2015). These data are provided every 16 days on a 250-m grid. For each season we clipped the NDVI data to the extent of the population's range and treated each pixel as a separate time series. We calculated the annual vegetation productivity at each pixel as the small integral value of NDVI (SIV of NDVI) using the TIMESAT software ver. 3.3 (Jönsson and Eklundh 2004). The SIV of NDVI captures the total area under the NDVI curve between the start and end of the growing season, above the baseline NDVI level (Wessels et al. 2011; further details in the Supporting information). For each season, we averaged the SIV of NDVI over all pixels to provide a measure of the average vegetation productivity across the population's range. Hereafter, we refer to this population-wide average as the SIV of NDVI.

Statistical analyses

Climate and vegetation productivity trends

To test for directional trends in temperature, rainfall, and SPEI-6 over the study period we applied Mann-Kendall trend tests to time series and used Sen's slope to estimate the linear rate of change per year (β_{Sen}). To allow for non-linear changes in temperature and rainfall we also specified a bivariate additive model (GAM) with monthly total rainfall and monthly mean maximum daily air temperature set as Gaussian response variables. The CPC temperature data in this model covered the period from 1979, the GPCP rainfall data the period from 1983. Rainfall was $\log(x+1)$ -transformed to normalise its right-skewed distribution. To allow for each month to have its own temporal trend, we included a month-specific smoother for the effect of year, choosing thin-plate regression splines as the marginal bases ($k=4$). We also included month as a parametric categorical variable so that each smoother was centred about its own long-term mean. The bivariate specification allowed us to also estimate the residual correlation between rainfall and temperature at a monthly scale. The GAM was fitted using the 'mgcv' R package (www.r-project.org, Wood 2011). To identify periods of significant change in each monthly time series, we evaluated the first derivatives of the fitted splines and their associated

confidence intervals using the method of finite differences (Simpson 2023). The rate of change at each evaluated point was considered significant where the 95% CIs of the derivative did not overlap zero.

To quantify the relationship between rainfall and annual vegetation productivity at our study site, we correlated the SIV of NDVI against annual site-measured rainfall. We also tested for a directional trend in the SIV of NDVI with a Mann–Kendall trend test.

Demographic trends

To test for directional trends in population density, mean group size, and in the various demographic parameters, we applied Mann–Kendall trend tests and estimated Sen's slopes. Population density and mean group size were treated as monthly series, whereas all reproductive and survival parameters were treated as yearly time series that represented the mean value across all groups in each breeding season. As various demographic measures appeared to decrease midway through the time series, we used Pettitt's test to identify any sudden change points. Pettitt's test is a non-parametric method that uses the Mann–Whitney statistic to test whether two periods of a time series come from the same distribution. The test returns the most probable change point and its associated significance level.

Effects of climate on population dynamics, reproduction and survival

We examined the effects of climate variability on population dynamics and on yearly measures of reproduction and survival using multiple regressions. Population dynamics were modelled as the proportional change in population density ($n=20$ years) or mean group size ($n=25$ years) between years (July to July). Reproductive and survival measures were modelled as the mean group-level response in each year ($n=25$ years), testing 1) the number of dominant female pregnancies, 2) the number of litters born the dominant female, 3) the number of pups emerging from the birth burrow, 4) recruitment: the number of pups surviving to independence, 5) pup survival: the proportion of pups surviving from emergence to independence, and 6) non-pup survival: the proportion of juveniles, subadults and adults surviving in the group across the year. For each measure we considered the effects of temperature, rainfall, and SPEI-6 over a range of timescales with the aim of identifying the most important climatic variable, and its most important window, in each case. For rainfall, we considered early breeding season rainfall (Sep–Nov), total breeding season rainfall (Sep–Apr), and two-yearly rainfall (summed over current and previous year; all log-transformed); for temperature, we considered the mean maximum summer air temperature (Dec–Apr) and the mean maximum yearly air temperature (Jul–Jun); and for SPEI we considered the mean SPEI-6 over the previous one or two years. All models also included a term for the population density or the mean group size at the start of the year to allow for short-term dependencies in population dynamics. When modelling annual measures of reproduction and

survival, we included group size as a quadratic effect when it increased model performance. Preliminary analyses suggested that considering density or group size effects over longer lags did not provide additional explanatory power. For each response variable we compared alternative models using Akaike's information criterion corrected for small sample size (AIC_c), and to compare the relative strength of the effects across models we standardised predictor variables to unit variance before model fitting.

We also repeated the linear regression analyses with year-detrended variables to decouple the effects of year and climate on the climate–demography relationships - especially involving temperature and SPEI. This involved regressing the residuals of independent regressions fitted on year (Iler et al. 2017).

Body mass trends

As body mass has been shown to be an important mediator of meerkat demography, we investigated long-term trends in adult body mass. We focused on adults because juveniles and subadults will still have been growing and any annual measure of mass would therefore be dependent upon the age distribution of individuals within these age classes. For each adult, we calculated their mean body mass in each year and then took the mean of these values to represent the population-level mean. We also repeated the process in each quarter of the year to see whether any body mass trend was more pronounced in certain periods of the year. We excluded any weights from pregnant females, and because males and females are monomorphic, the two sexes were treated jointly.

Group extinctions

Previous studies have shown that small meerkat groups are more likely to go extinct (Duncan et al. 2021). We confirmed this relationship with our longer time series and tested whether the probability of group extinction varied over time. Specifically, because the average size of groups fell after the 2012/2013 breeding season, we compared extinction rates either side of this time point. To maintain consistency with the rest of the study, we focussed on groups that were established in the population at the start of each breeding season. This meant excluding small groups that formed and failed within a single year, thus removing the strong influence of founding events on extinction probability (Duncan et al. 2021). We classified group extinctions based on field data following the same criteria as Duncan et al. (2021). In the small number of cases where group fate was uncertain, or where groups were abandoned by researchers for logistical reasons, we excluded the final year of data for those groups.

We modelled annual group extinction probability using generalised linear mixed effects models (GLMM) with a binomial response (0/1). The first model included group size as the sole fixed effect. The second model included time-period as a single categorical variable, with pre 2012/2013 covering the breeding seasons before July 2012, and post 2012/2013 covering the 2012/2013 season onward. Both models included a random effect of group identity and were fitted using the 'glmmTMB' package (Brooks et al. 2017).

The dataset included 274 group-years and 44 groups. 12 groups were still present as of July 2023.

For all statistical models we used model validation plots to confirm the independence and normality of the residuals. For GLMMs, this involved using the 'DHARMA' package (Hartig et al. 2022) to simulate scaled residuals from each model. Statistical analyses, data handling, and plotting were carried out in R ver. 4.4.1 (www.r-project.org). The R code used for analyses is provided at <https://github.com/JThor1990/Meerkat-Population-Regulation>.

Results

Temperature, rainfall, and vegetation productivity

Average daily maximum air temperatures increased significantly over the study period ($\beta_{\text{Sen}} = 0.11^{\circ}\text{C year}^{-1}$ [95%CI: 0.05, 0.16], $z = 3.74$, $p < 0.001$, $n = 372$). The most pronounced temperature rises occurred in the last two decades and significant increases were detected in all months of the year (Fig. 1). Average daily maximum temperatures rose by between 1.51°C and 3.19°C since 1993, corresponding to a 5–10% increase in the hottest months (Nov–Feb) and an 11–14% increase in the coolest months (Jun–Aug). These rising temperatures coincided with a dramatic increase in the number of hot days annually, when air temperatures exceeded important physiological thresholds for meerkats (Supporting information). The number of days over 37.5°C , for example, tripled from 25 to almost 75 days year^{-1} within three decades.

Since 1998, annual rainfall ranged from 115 mm to 705 mm (mean \pm SD = 297.4 ± 135.3), with most rain falling between October and April each year. Early and late summer rainfall showed higher variability (Sep–Nov coefficients of variability (CVs): 1.15–1.80, April CV = 1.15) than mid-summer rainfall (Dec–Mar CVs: 0.66–1.01). There has been no consistent trend in annual rainfall over the study period (onsite rainfall, $\beta_{\text{Sen}} = 5.37 \text{ mm year}^{-1}$ [95%CI: -12.02 , 1.44], $z = -1.66$, $p = 0.10$, $n = 25$; GPCP rainfall, $\beta_{\text{Sen}} = 0.84 \text{ mm year}^{-1}$ [95%CI: -4.22 , 4.75], $z = 0.21$, $p = 0.83$, $n = 30$), or over the last 40 years (GPCP rainfall, $\beta_{\text{Sen}} = 1.87 \text{ mm year}^{-1}$ [95%CI: -1.11 , 4.66], $z = 1.31$, $p = 0.19$, $n = 41$). Nor has there been a significant decline in most months of the year, except for October (MK test, $p = 0.013$; Fig. 1), which contributed towards a trend for less rainfall in early summer ($\beta_{\text{Sen}} = -1.27 \text{ mm year}^{-1}$ [95%CI: -2.70 , 0.26], $z = -1.72$, $p = 0.086$, $n = 26$). A decline in early summer rainfall was also present in the remotely sensed data (GPCP rainfall, $\beta_{\text{Sen}} = -0.75 \text{ mm year}^{-1}$ [95%CI: -1.57 , -0.02], $z = -2.09$, $p = 0.037$, $n = 40$; Fig. 1). Increases in rainfall were associated with lower maximum temperatures (GAM residual correlation: mean = -0.59).

Annual vegetation productivity, as measured by the SIV of NDVI, was strongly correlated with annual rainfall (Pearson's $r = 0.72$ [95%CI: 0.44, 0.87], $df = 21$, $p < 0.001$; Fig. 2). Like rainfall, the SIV of NDVI varied widely between years without a consistent trend over time ($\beta_{\text{Sen}} = 0.015/\text{year}$ [95%CI: -0.014 , 0.040], $z = 1.11$, $p = 0.27$, $n = 23$; Supporting

information). Despite there being no trend in annual rainfall or vegetation productivity, increasing air temperatures contributed to a decline in SPEI over the study period (MK test, $z = -10.83$, $p < 0.001$, $n = 319$). This site-based decline was also evident in the remotely sensed SPEI data (Fig. 1B, MK test, $z = -4.70$, $p < 0.001$, $n = 541$). The decade starting in July 2010 was especially dry, with the Kalahari experiencing moderate drought conditions for 29.8% of the decade ($\text{SPEI-6} \leq -1$) - nearly double the background rate of 15.7%.

Trends in group size and population density

Population density and mean group size fluctuated over time and experienced several crashes (Fig. 3). The population crash over the 2012/2013 breeding season marked a regime change in the central tendency of both time series after which population density and average group size were consistently lower than they were previously (Pettitt's test, maximal \hat{u} on 1 Nov 2012 and 1 Dec 2012 respectively, $p < 0.001$). Before 2013, average group size was 15.82 individuals (SD = 3.74), compared to 11.74 individuals after (SD = 3.50, t-test, $t = 11.42$, $df = 305.4$, $p < 0.001$). Similarly, average population density decreased from 9.38 individuals km^{-2} (SD = 5.25) to 5.25 individuals km^{-2} after 2013, a 44% decline (SD = 1.52; t-test, $t = 17.09$, $df = 215.2$, $p < 0.001$). Overall, group size and population density both declined significantly over time, as did group density (Table 1).

Trends in demographic rates

Several demographic rates also showed consistent directional trends (Table 1, Fig. 3B). Despite stable rates of pregnancy in dominant females over the study period, an increased incidence of failed pregnancies led to a decline in the number of litters born to dominant females (Table 1, Supporting information). The number of subordinate pregnancies also declined as group size fell (Table 1). However, as most subordinate pregnancies fail, the total number of litters born to subordinates showed little variation around the long-term average of 0.88 ± 0.34 litters per group per year (Table 1). Subordinates contributed $18.4 \pm 7.5\%$ of recruited pups, on average (annual mean \pm SD).

Though dominant females birthed fewer litters over time, the average number of pups emerging from each group's breeding burrows each year did not decline significantly, whereas the survival of pups between emergence and nutritional independence (recruitment) declined strongly (Fig. 3B) and was estimated at 0.59% per year (Table 1). Although not statistically significant, it contributed to a decrease in the average number of pups recruited into each group over time (Table 1). Pup survival was particularly low following the 2010/11 breeding season (Fig. 3B, Pettitt's test, $p < 0.001$), with mean annual survival dropping to 72.8% (SD = 10.3%), down from 87.0% (SD = 5.2%) previously (t-test, $t = 4.40$, $df = 18.01$, $p < 0.001$).

There were also significant declines in the survival of juveniles, subadults and adults (Table 1). Grouping all these 'non-pup' age-classes together, annual survival rates across

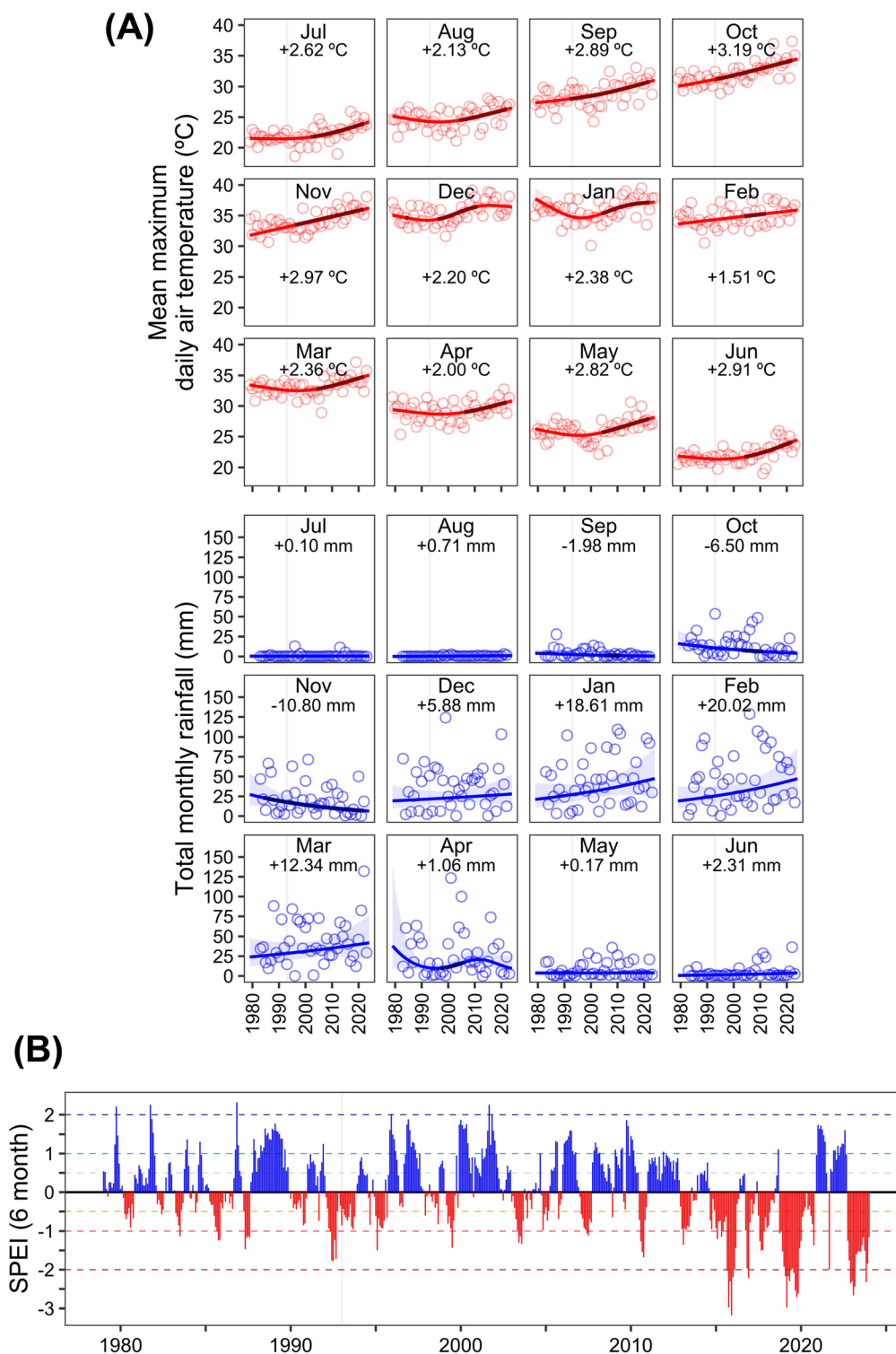


Figure 1. Long-term changes in temperature, rainfall, and SPEI in the Kalahari. For temperature and rainfall (A), points show the mean maximum daily temperature (upper) and the total rainfall (lower) in each month. Lines and shaded areas show the predicted mean trendline \pm 95% confidence intervals as estimated by a general additive model. Periods of significant change within each monthly time series are indicated by the thicker, darker line: where the first derivative of the smooth is non-zero. Numbers indicate the predicted change in temperature and rainfall between the start of the Kalahari Meerkat Project in 1993 (thin vertical line) and 2023, for each month. (B) Changes in SPEI reflect the dryness of the Kalahari at our study site. Cases where SPEI-6 falls below -1 and -2 represent moderate or extreme drought conditions, respectively. All trends are produced from remotely sensed datasets to allow for longer time series.

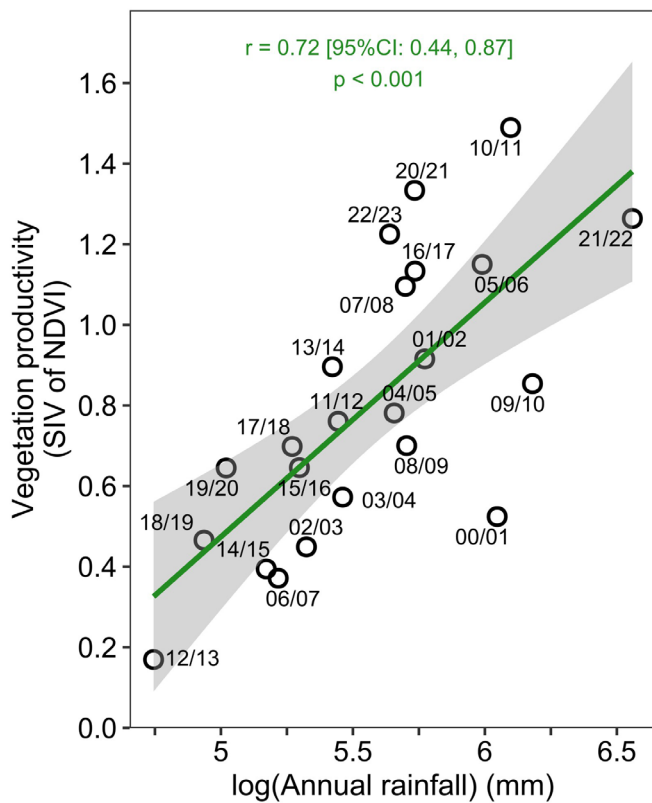


Figure 2. The correlation between the total annual rainfall and the average primary productivity of vegetation across the study area. The SIV of NDVI refers to the small integral value of NDVI curve, relative to the baseline level. We calculated this value for all pixels that fell within the home ranges of established meerkat groups each year and averaged them. The productivity data are presented as a time series in the Supporting information. Rainfall represents the total rainfall measured onsite.

the population declined by 0.51% per year ($\beta_{\text{Sen}} = -0.0051$ [95%CI: $-0.0090, -0.0019$], $z = -2.64$, $p = 0.008$, $n = 25$), and as in pups, survival rates were particularly low in the past decade (Fig. 2B; Pettitt's test, $p < 0.023$). Annual declines were estimated at 0.64% in juveniles, 0.46% in subadults, and 0.55% in adults.

Trends in adult body mass

The decline in adult survival coincided with significant reductions in adult body mass (Fig. 3C, $\beta_{\text{Sen}} = -2.15 \text{ g year}^{-1}$ [95%CI: $-3.26, -1.03$], $z = -3.01$, $p = 0.003$, $n = 25$). Body mass declines were especially strong in winter (May–Aug: $\beta_{\text{Sen}} = -1.80 \text{ g year}^{-1}$ [95%CI: $-2.99, -0.49$], $z = -2.59$, $p = 0.010$, $n = 25$; Supporting information) and early summer (Sep–Nov: $\beta_{\text{Sen}} = -2.48 \text{ g year}^{-1}$ [95%CI: $-3.80, -0.63$], $n = 25$, $z = -2.64$, $p = 0.008$; Supporting information). In the later years of our study, individuals entered summer approximately 60 g lighter ($\sim 10\%$) than at the study's onset and continued to lose body mass throughout early summer if the rains were delayed, as occurred repeatedly between 2010 and 2020

(Fig. 1). Once the rains arrived, which was usually the case by December, individuals were able to gain body mass relatively quickly and body mass declines were less pronounced in mid- to late summer as a result (Dec–Apr: $\beta_{\text{Sen}} = -1.22 \text{ g year}^{-1}$ [95%CI: $-3.80, -0.63$], $z = -1.80$, $p = 0.072$, $n = 25$).

Effects of climate on population dynamics

Annual changes in population density were strongly associated with variation in rainfall and the density at the start of the year (Fig. 4). Population density increased after years of high rainfall (Table 2; $\beta = 0.21 \pm 0.05$, $p < 0.001$) and decreased when the density at the start of the year was high ($\beta = -0.16 \pm 0.05$, $p = 0.005$), and the two terms together explained 59% of the variation in the response. Mean yearly SPEI was also positively associated with the change in density but provided less explanatory power than the best supported rainfall model ($R^2 = 0.33$, $p = 0.05$). In contrast, changes in population density were not significantly associated with variation in air temperature and the inclusion of temperature in models brought only minor increases in explained variation (Table 2). There was a weak correlation between the temperature variables and the start-of-year density (Pearson's $r \geq -0.37$), but the effects of temperature remained non-significant when modelled without a density term ($p \geq 0.55$).

Models of the change in mean group size across years also indicated that rainfall was relatively more important than SPEI, which was relatively more important than temperature, in turn (Table 2). The direction and magnitude of these effects were also similar. Increases in mean group size were associated with high breeding season rainfall and relatively wet years, while temperature variations had no significant effect (Fig. 4). Controlling for rainfall, average group size declined sharply in years where the average group size at the start of the year was high ($\beta = -0.16 \pm 0.04$, $p = 0.001$; Fig. 4).

Effects of climate on reproduction and survival

Examining the candidate sets of models revealed mixed support for the associations between climate variables and annual measures of reproduction and survival. The number of dominant female pregnancies was not associated with rainfall, temperature, or SPEI, but was negatively associated with group size ($\beta = -0.21 \pm 0.09$, $p = 0.029$, $R^2 = 0.23$, Supporting information). In contrast, the number of litters born to dominant females per year, as well as with the numbers of pups that emerged from the natal burrow, and that were recruited to each group, was significantly associated with variation in rainfall and temperature (Fig. 5, Supporting Information). For each of these reproductive measures, the effects of rainfall were always positive while those of temperature were always negative, and in all cases, the best-supported model was that which included the total breeding season rainfall (Sep–Apr). The importance of this rainfall measure for reproductive output was confirmed in multiple regressions fitted to detrended data: where it retained a strong positive relationship with the number of litters per year born to the dominant female

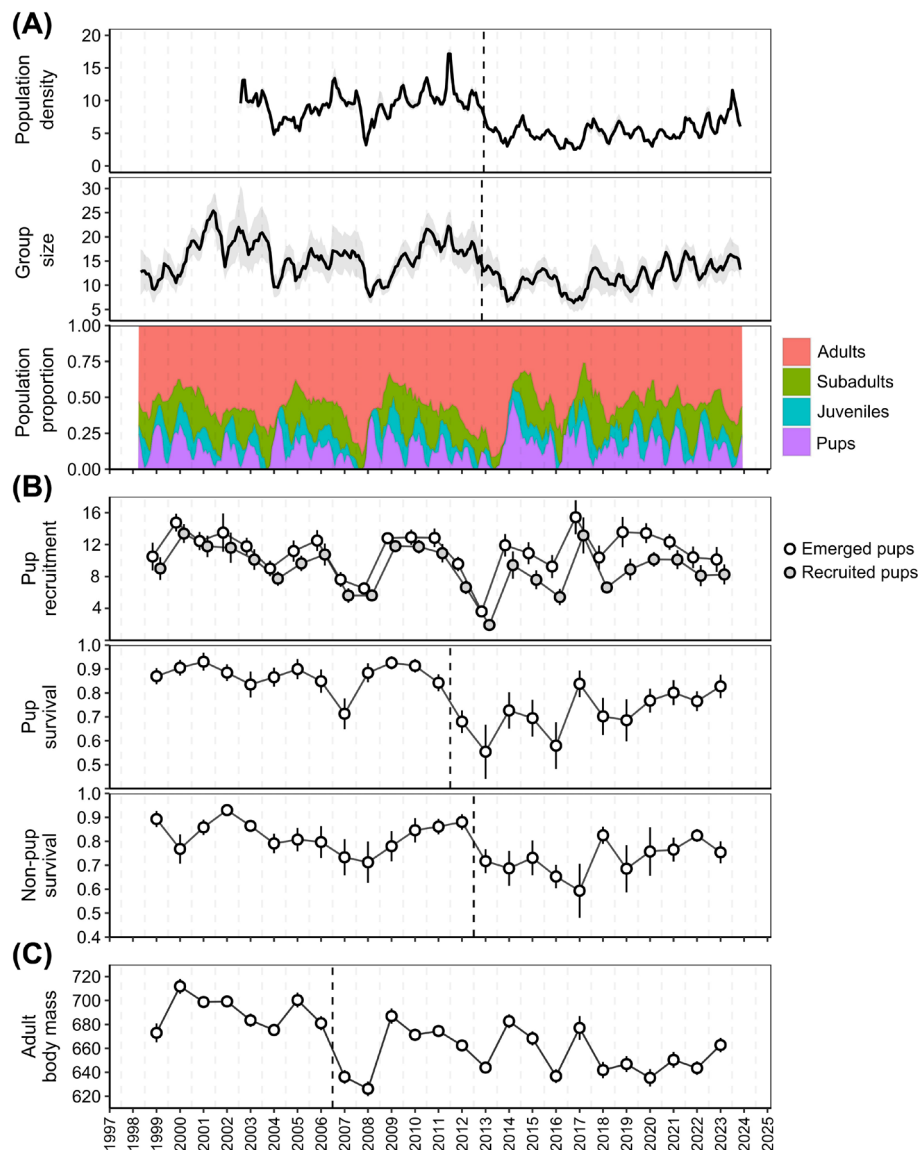


Figure 3. Fluctuations in population density, average group size, recruitment, survival, and adult body mass over time. (A) Population density, group size, and age structure through time. Uncertainty in population density and average group size were estimated through jackknifing and bootstrapping, respectively (shaded areas show 95% CI). (B) The recruitment and survival of pups, and the survival of all 'non-pup' age classes in each year, averaged over each group (mean \pm SEM). Non-pup survival indicates the proportion of juveniles, subadults and adults that survived in their group from the start of one breeding season to the start of the next breeding season (1 July to 30 June). Pup survival indicates the proportion of emergent pups within a given breeding that reached nutritional independence at 3 months. (C) Average adult body mass (mean \pm SEM) in each breeding season. Where significant ($p < 0.05$), the solid vertical dashed lines mark a statistically identified changepoint in each time series (Pettitt's test).

($\beta = 0.23 \pm 0.07$, $p = 0.005$, $R^2 = 0.34$), the number of pups that emerged ($\beta = 1.25 \pm 0.42$, $p = 0.007$, $R^2 = 0.47$), and the number of pups recruited ($\beta = 1.67 \pm 0.38$, $p < 0.001$, $R^2 = 0.58$), while continuing to explain the most variation in model comparisons (Supporting information). Given the strong positive relationship between rainfall and SPEI, increases in SPEI mostly showed positive effects on reproductive measures, but the effects were often non-significant and explained less variation than the best-supported models involving rainfall or temperature. For the reproductive

measures, average maximum summer temperatures and average maximum yearly temperatures usually explained similar amounts of variation so that the relative importance of the two temperature variables could not be separated. The negative relationship between temperature and reproductive performance was strongest for the number of pups recruited per group (Fig. 5) and this was the only reproductive measure for which the temperature variables retained significance after detrending (mean annual max temp: $\beta = -1.22 \pm 0.52$, $p = 0.029$, $R^2 = 35$). After accounting for the positive effect of

Table 1. Trends in demographic parameters over the 25-year study period (1998–2023). The population change parameters refer to the proportional change in each parameter from one year to the next, whereas the reproductive and survival parameters represent the average value across all established groups in the population at the start of each year (July). For each parameter, the annual rate of change was calculated as Sen's slope (β_{Sen}), with units provided where necessary. The Mann-Kendall trend test provides a significance test for the presence of a directional trend.

Demographic parameter (time series length)	Annual rate of change (β_{Sen} [95% CI])	Mann-Kendall trend test	
		z-statistic	p-value
Population change			
Average group size (n=311)	-0.178 [-0.238, -0.116]	z=-5.79	p < 0.001
Population density (meerkats km ⁻² , n=259)	-0.223 [-0.273, -0.172]	z=-7.89	p < 0.001
Group density (groups km ⁻² , n=259)	-0.009 [-0.012, -0.007]	z=-7.72	p < 0.001
Reproductive parameters (n=25)			
Dominant female pregnancies	-0.012 [-0.039, 0.019]	z=-0.72	p=0.47
Subordinate female pregnancies	-0.083 [-0.142, -0.035]	z=-3.34	p=0.001
Dominant female litters	-0.024 [-0.049, 0.000]	z=-2.01	p=0.044
Subordinate female litters	-0.007 [-0.030, 0.013]	z=-0.98	p=0.33
Number of pups emerging	-0.033 [-0.184, 0.100]	z=-0.30	p=0.76
Number of pups recruited	--0.100 [-0.240, 0.051]	z=-1.40	p=0.16
Survival parameters (n=25)			
Pup survival (%)	-0.648 [-1.171, -0.191]	z=-2.73	p=0.006
Juvenile survival (%)	-0.644 [-1.259, -0.205]	z=-2.29	p=0.022
Subadult survival (%)	-0.458 [-1.258, 0.124]	z=-1.38	p=0.17
Adult survival (%)	-0.549 [-1.036, -0.111]	z=-2.36	p=0.018

rainfall, group size displayed a u-shaped quadratic relationship with the number of pups that emerged from and that were recruited to each group per year (Fig. 5).

For the survival of all age classes, the effects of rainfall and SPEI were positive while those of temperature were negative (Supporting information). For pup survival, the model including total breeding season rainfall provided most explanatory power ($\beta = 0.081 \pm 0.015$, $p < 0.001$, $R^2 = 0.56$), followed by the mean maximum annual temperature ($\Delta\text{AIC} = 9.03$, $\beta = -0.077 \pm 0.022$, $p = 0.002$, $R^2 = 0.37$). There was no effect of group size on pup survival when the data were aggregated across groups (Fig. 5). The relationship between detrended breeding season rainfall and detrended pup survival remained strongly positive ($\beta = 0.065 \pm 0.013$, $p < 0.001$, $R^2 = 0.64$), whereas the effects of temperature were diminished (annual temperature: $\beta = -0.032 \pm 0.020$, $p = 0.13$, $R^2 = 0.12$; summer temperature: $\beta = -0.035 \pm 0.018$, $p = 0.060$, $R^2 = 0.17$), indicating that interannual variation in temperature could only explain modest amounts of variation around the overall decline in pup survival. Variation in adult survival was not significantly associated with any climate variables but variation in juvenile and subadult survival showed a negative association with temperature (summer temperature: $\beta = -0.040 \pm 0.015$, $p = 0.017$, $R^2 = 0.50$; annual temperature: $\beta = -0.044 \pm 0.018$, $p = 0.024$, $R^2 = 0.49$) and a positive association with rainfall in the breeding season ($\beta = 0.031 \pm 0.015$, $p = 0.055$, $R^2 = 0.45$). The effects of temperature on the combined survival of juveniles and sub-adults retained their importance after detrending, while those of rainfall were reduced (Supporting information). In juveniles and subadults, and in adults, group size had a strong positive effect on annual survival, which translated into a strong positive effect on non-pup survival overall (Fig. 5; $\beta = 0.049 \pm 0.013$, $p < 0.001$).

For all demographic parameters, including the best supported rainfall and temperature variables in the same multiple regression did not lead to significant improvements in model fit, and only generated very small increases in explained variation (Supporting information).

Group extinctions

Small groups were more likely to go extinct than large groups (Fig. 6A, $\beta = -0.10 \pm 0.04$, $z = -2.82$, $p = 0.005$). As average group sizes were smaller in the years following the 2012/2013 population crash than they were beforehand, rates of group extinction were also higher after 2012/2013 (Fig. 6B, $\beta = 1.08 \pm 0.50$, $z = 2.17$, $p = 0.03$).

Discussion

Against a backdrop of long-term warming in the Kalahari Desert, our analyses of 25 years of demographic data show that rainfall is the primary environmental regulator of meerkat population dynamics. By strongly affecting the production of pups and their survival to nutritional independence, rainfall controls recruitment, which is the major contributor to changes in group size and population density. Adult mortality, by comparison, varied little between years and its influence on population dynamics was small, as earlier work suggested (Bateman et al. 2012).

Changes in temperature were also associated with several vital rates, including the survival of pups, juveniles and subadults. However, the effects of temperature were generally weaker than those of rainfall and were further diminished once temperature and demographic time series were detrended (decoupling interannual variations from long-term trends), as well as when temperature and rainfall

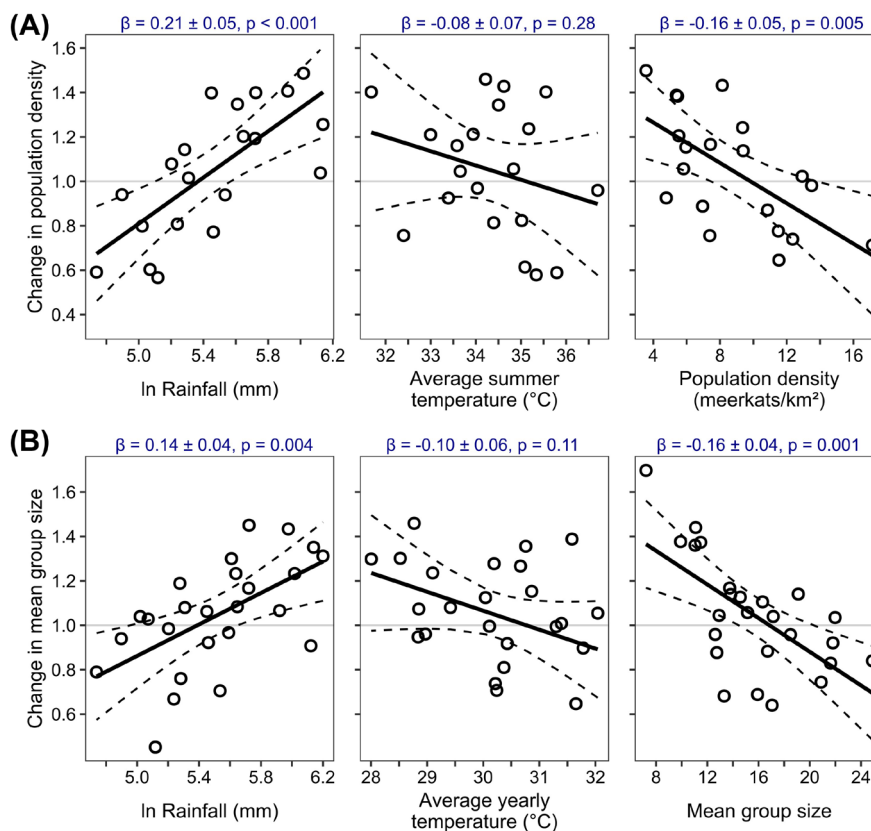


Figure 4. Effects of climate, population density, and group size on annual changes in population density (A) and mean group size (B). The response variable represents the proportional change in the population density or mean group size from July to July. Slopes and their associated 95% confidence intervals display the predictions from multiple regressions presented in Table 2. Rainfall represents the ln rainfall across the breeding season (Sep–Apr), whereas temperature represents either the mean maximum summer temperature (Dec–Apr) or the mean maximum yearly temperature (Jul–Jul) depending on which timescale explained more variation. Predictions for the effects of temperature and rainfall come from regressions that also included an effect of density or mean group size at the start of the year, and predictions for the effects of density and group size come from regressions that included rainfall. Points are displayed as partial residuals so that the effects of the focal variable can be seen independently. Standardised slopes (\pm SEM) and their significance are provided above each panel.

variables were modelled together. Consequently, though rising temperatures over the past three decades have affected population density and contributed to the decline in meerkat numbers over this period (Paniw et al. 2019, 2022), changes in temperature have not had as strong an impact as might be expected from the presence of long-term trends alone.

The secondary impact of temperature contrasts with the situation in some bird species in the Kalahari, where high temperatures have been shown to strongly depress reproduction and survival and have been considered a primary driver of changes in population size (Conradie et al. 2019, Ridley et al. 2021, Pattinson et al. 2022). The demographic effects of high temperatures on birds may be particularly pronounced because birds are often small and have high mass-specific metabolic rates (Clarke et al. 2010). However, since birds and small mammals show broadly similar heat tolerances (McKechnie and Wolf 2019), differences in their susceptibility to high temperatures could also reflect alternative heat-avoidance strategies. For example, unlike most small mammals, relatively few birds in arid areas take refuge underground during the hottest parts of the day (Williams et al.

1999), and a much higher proportion of bird species are diurnal. There is also a rich history of studying mammalian population dynamics in arid environments, driven by counts of ungulates in Africa (Ogutu et al. 2014, Owen-Smith 2021), a general interest in rodent population regulation (Brown and Ernest 2002, Holmgren et al. 2006), and the widespread adoption of camera trapping (Greenville et al. 2017). In contrast, research on arid-zone birds has often focussed on questions related to physiology and behaviour, which typically requires shorter-term datasets. Consequently, fewer studies of arid-zone birds appear to have provided the long-term datasets needed to distinguish the demographic effects of temperature from those of rainfall over extended periods. When such data has been analysed, rainfall frequently emerges as the main environmental forcing for birds as well (Grant et al. 2000, Altwegg and Anderson 2009, Iknayan and Beissinger 2018), though there are exceptions (Cruz-McDonnell and Wolf 2015, Ridley et al. 2021).

Previous studies have demonstrated the importance of rainfall for meerkat demography (Bateman et al. 2011, 2013, Ozgul et al. 2014, Paniw et al. 2019, Groenewoud and

Table 2. Linear regression summaries and AICc ranking for models comparing the effects of different climate variables on meerkat population dynamics, estimated via proportional changes in population density (2003–2023) and mean group size (1998–2023) between years. Models were ranked by the change in AICc (Δ AICc), which indicates the contrast from the most parsimonious model. We also present the standardised slopes (β) for each climate variable and their associated p-values, as well as the coefficient of determination (R^2) for each model. All models included a term for the population density or the mean group size at the start of the year, both of which showed a significant negative relationship with population change throughout.

Climate variable	Annual population density change (n=20 years)					Annual group size change (n=25 years)				
	Δ AICc	Rank	$\beta \pm$ SE	R^2	p-value	Δ AICc	Rank	$\beta \pm$ SE	R^2	p-value
Null	11.11	4	–	0.16	–	7.04	6	–	0.24	–
Rainfall										
Early season rainfall (Sep–Nov)	13.25	7	0.06 \pm 0.07	0.20	0.36	9.32	8	0.04 \pm 0.05	0.26	0.48
Breeding season rainfall (Sep–Apr)	0.00	1	0.21 \pm 0.05	0.59	<0.001	0.00	1	0.14 \pm 0.04	0.49	0.004
Combined two-year rainfall	2.52	2	0.22 \pm 0.06	0.53	0.002	1.80	2	0.14 \pm 0.05	0.45	0.008
Temperature										
Mean maximum summer temperature (Dec–Apr)	12.89	6	–0.08 \pm 0.07	0.21	0.28	7.52	7	–0.08 \pm 0.05	0.31	0.15
Mean maximum annual temperature (Jul–Jun)	13.83	8	–0.05 \pm 0.08	0.18	0.54	6.98	5	–0.10 \pm 0.06	0.32	0.11
SPEI										
Mean annual SPEI-6 (Jul–Jun)	9.83	3	0.15 \pm 0.07	0.33	0.055	3.61	3	0.13 \pm 0.05	0.41	0.020
Combined two-year mean SPEI-6	11.22	5	0.15 \pm 0.09	0.28	0.11	5.35	4	0.14 \pm 0.06	0.37	0.048

Clutton-Brock 2021), but the protracted effects of droughts have not been well described. By working at an annual resolution, we show that the clearest effects of rainfall occurred in very dry years, when group sizes fell sharply, and population density crashed. One of the most pronounced collapses occurred during 2012/2013 breeding season, which was also the year with the lowest rainfall in our study (115 mm). Across this specific year, dominant females displayed low pregnancy rates and birthed few pups, and the pups that did emerge had low survival, which together resulted in extremely low recruitment. With such low recruitment, group sizes fell, some groups went extinct, and population density halved. Subsequently, intermittent years of low rainfall and low rates of recruitment maintained the density of the population below its previous level.

There are three main conclusions to be drawn from these patterns. First, it suggests that several consecutive years of above-average rainfall are needed for effective growth of the meerkat population. Second, the presence of similar relationships between rainfall and population density at our reserve and in the Kgalagadi Transfrontier Park suggests that the environmental regulation of our meerkat population is representative of meerkats in the wider Kalahari region. And third, it suggests that changes in the frequency and intensity of droughts under climate change are likely to be the major environmental factor determining the stability of the meerkat population. If low rainfall years in the Kalahari become more frequent, as most climate models predict with reasonable confidence (Archer et al. 2018), then our meerkat population, and others in the region, could be particularly at risk.

The demographic impact of years of low rainfall from 2012 onwards may have been compounded by consistently delayed rainfall in the early breeding season. Meerkats, like many

other animals in the Kalahari, anticipate the arrival of the summer rains (Lovegrove 2021). Dominant females normally fall pregnant in midwinter so that the birth of their first litter of the season overlaps with the first effective rainfall events in September and October. If, however, the rains don't arrive at this time, then most of the first litters fail and the population loses its first cohort of recruits. Worryingly, a large majority of climate projections identify early summer as the main period of the year in which future rainfall declines will occur (Munday and Washington 2019). This suggests that delays in summer rainfall could become a more frequent challenge for the animals of the Kalahari to contend with; though the extent to which species will be affected is likely to depend upon their diet and their reliance on free-standing water, as well as other aspects of their life history (Ogutu et al. 2014, Lovegrove 2021, Owen-Smith 2021).

In the case of meerkats, we speculate that the slow recovery of the population after very dry years is partly a consequence of the species' breeding system. Meerkats are cooperative breeders where the reproductive output of groups is largely restricted to the dominant female. As dominant females typically produce only two litters per year in which pups are successfully weaned (1.87 ± 0.99 , mean \pm 1SD), there is limited scope for rapid population growth compared to less skewed societies where all adult females will breed under favourable conditions. In addition, the rearing of pups is reliant on the efforts of non-breeding helpers who are responsible for most of the protection and feeding of young during their first three months of life. The amount of food that pups receive as well as their growth and survival vary with the ratio of helpers to pups (Clutton-Brock et al. 2001b), which will often be low when group sizes are small, as occurs following low rainfall years. While our results suggest that small groups can be

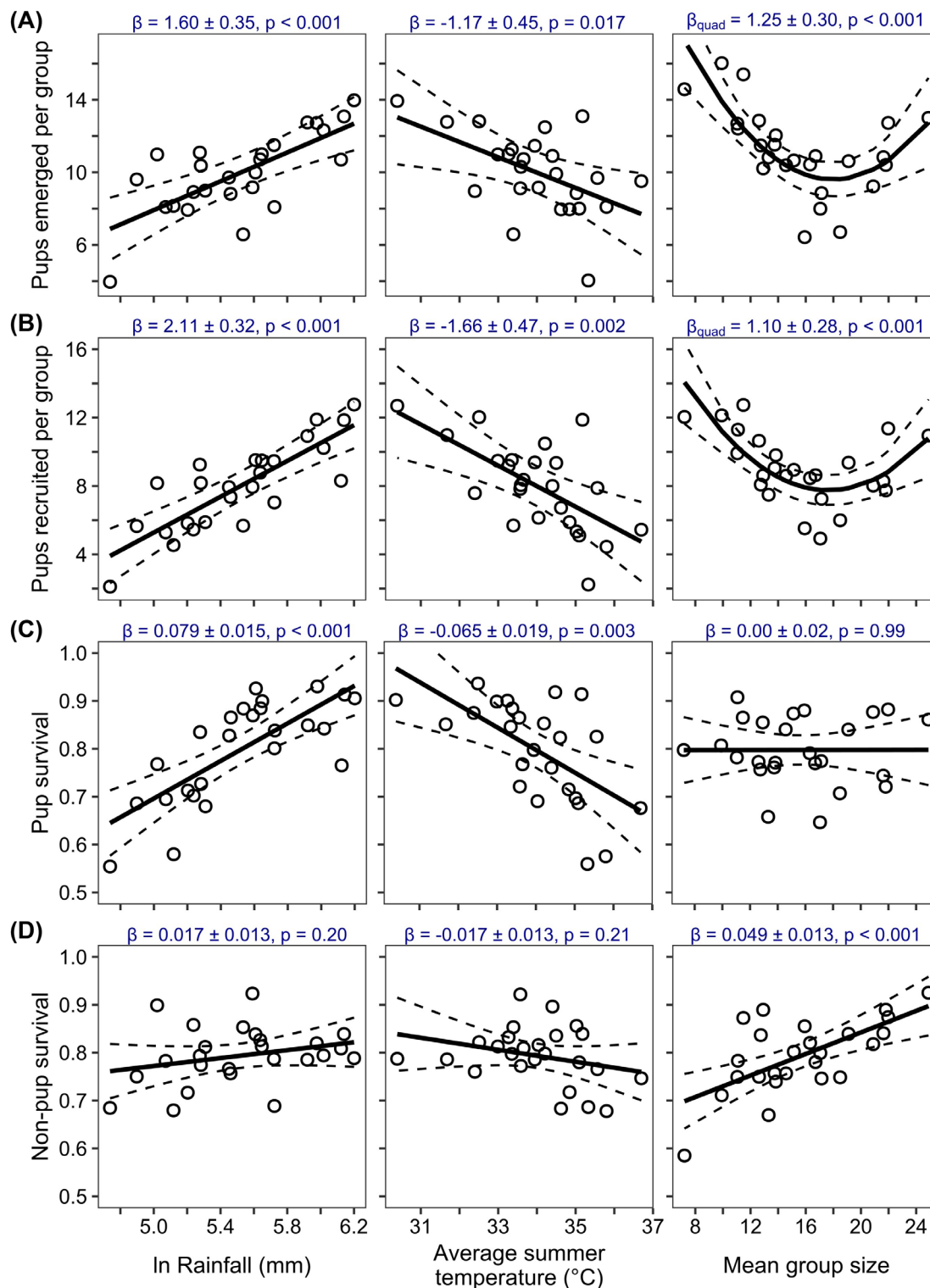


Figure 5. Effects of climate on annual measures of reproduction and survival. Response variables represent the mean number of pups that emerged from the natal burrow (A) or were recruited (B) to each group per year, and the mean survival of pups (C) or non-pups (juveniles, subadults and adults, (D)) in each group per year. Slopes and their associated 95% confidence intervals display the predictions from multiple regressions. Rainfall represents the ln rainfall across the breeding season (Sep–Apr), whereas temperature represents the mean maximum summer temperature (Dec–Apr). Predictions for the effects of temperature and rainfall come from regressions that also included an effect of mean group size at the start of the year, and predictions for the effects of mean group size come from regressions that included rainfall. Points are displayed as partial residuals so that the effects of the focal variable can be seen independently of the other modelled terms.

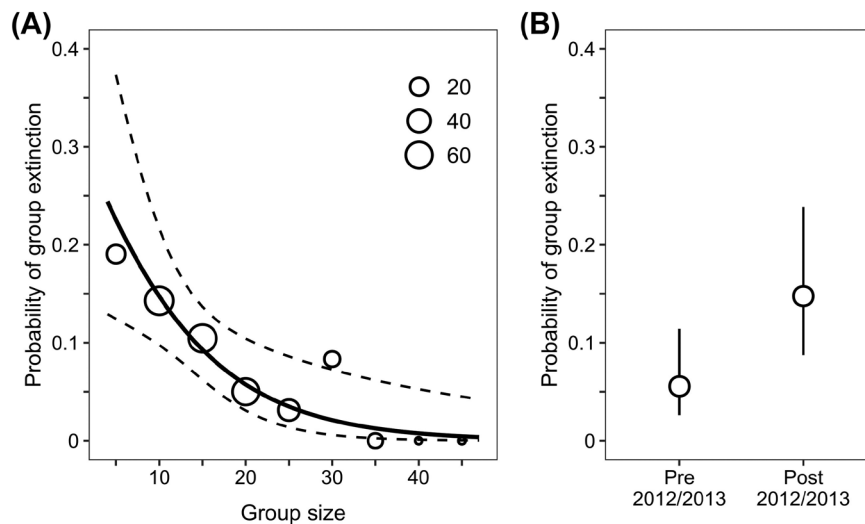


Figure 6. Group extinctions. The annual probability that established groups went extinct declined with increasing group size (A). As the average size of groups were lower after the 2012/2013 breeding season than they were before (Figure 2A), the annual probability of group extinction was also higher after 2012/2013 (B). Both panels present the predicted annual probability of group extinction \pm 95% confidence intervals, as estimated by GLMMs. In (A), the points are sized according to the total number of group-years and for the purpose of plotting, the raw data are presented in increments of five.

relatively productive (Fig. 5), we treated group size as the average group size across all groups in the population. If, instead, we analysed the responses of individual groups directly, which would commonly include groups of less than five individuals, then it would become apparent that small groups typically struggle to raise offspring successfully (Groenewoud and Clutton-Brock 2020). This is also the case in other singular cooperative breeders (Ebensperger et al. 2012) and would be expected to slow population recovery following drought years (Angulo et al. 2018).

The mechanism through which rainfall affects demography probably involves changes in food supply. In support of this argument, we show that variation in annual rainfall at our field site is closely correlated with the total vegetation productivity across the ranges of the meerkat groups in each year. Vegetation productivity, in turn, is expected to be closely correlated with the abundance of insect herbivores that are the meerkats main food source (Doolan and MacDonald 1996). Importantly, the correlation between rainfall and vegetation productivity was strong despite their potentially complex relationship in arid environments, where both the timing and magnitude of discrete rainfall events are relevant (Ogle and Reynolds 2004). Future research can now look to confirm the causality of the relationships between NDVI, insect abundance, and meerkat foraging success.

Our analyses suggest that temperature is also having demographic effects on the meerkats, especially on the survival of pups, juveniles, and subadults. Nevertheless, by looking at the relative changes in density and group size from year to year, our results show that increased temperatures in particular years as well as rising temperatures across years have been associated with only modest reductions in population density and group size and, in both cases, these negative relationships failed to reach statistical significance. Moreover,

when the time series of temperature and specific vital rates were detrended by year, the magnitude of the temperature–demography relationships became weaker and the only vital rate that was still significantly associated with temperature after detrending was the survival of juveniles and subadults (though in several cases the correlations approached significance). In this specific case, we can be reasonably confident in the effect of increasing temperatures, whether direct or indirect.

In contrast, in cases where the biological significance of the temperature–demography relationship disappeared after detrending, the effects of temperature cannot be distinguished from those of year, and it is possible that co-occurring trends in other unmeasured variables were responsible for the correlated changes in demography. Though possible, we think that this is unlikely, as separate, targeted studies of our population have shown that high summer temperatures limit the daily foraging time of adults (Habicher 2009) and are associated with reductions in the growth and survival of pups (van de Ven et al. 2020). Physiological assays also suggest that meerkats become increasingly heat stressed once air temperatures exceed 35°C, with thermoregulatory costs rising significantly (Müller and Lojewski 1986). The number of days per year where temperatures have passed this threshold has climbed dramatically over the study period (Supporting information). Taken together, this would suggest that rising temperatures are impacting meerkats in the short-term, both behaviourally and physiologically. More work now needs to be done to understand why these effects have not translated into stronger consequences at the population-level.

The effects of variation in rainfall and temperature on animal populations can also be challenging to separate as the two variables are climatically interrelated and will often be closely correlated with each other. We found that this was the case in

our own data, with dry months being hotter than relatively cool months for a given time of year. We suspect that this is due to a combination of the cooling effect of rainfall and the reduced solar radiation that comes with increasing cloud cover. Given this close association, the independent effects of rainfall and temperature on the growth, reproduction and survival of animals may be expected to compound or potentiate one another (Bourne et al. 2020). It is not currently clear whether such interactions are at play in the meerkat population. As Kalahari winters are always cold and dry, and the hottest parts of each summer are almost always wet, testing for these interactions is not as straightforward as it might first seem, and will probably require relatively long time series.

Lastly, our analyses reiterate that meerkat numbers are also controlled by density dependent factors (Bateman et al. 2011, 2012). At the population level, density dependence was conventional and direct in form, with density declining in years that started out at high density. Because population density was very closely correlated with the average size of groups, it can be assumed that density dependence operates largely through the effects of group size on different demographic rates. Working under this assumption, we found that annual recruitment to groups declined with increasing group size (though there was a slight upturn at very large group sizes), while per capita adult mortality decreased. This suggests that recruitment falls as the average size of groups increases and is not offset by reductions in adult mortality, leading to reductions in the average size of groups and in population density. Because the number of litters born to dominant females did not vary with group size, yet fewer pups emerged from the burrow, the drop in recruitment could be attributed to heightened pup mortality in early life, much of which was probably caused by female infanticide (Young and Clutton-Brock 2006, Cram et al. 2019). If correct, this suggests that reproductive competition between females is having population-level consequences.

In conclusion, our study highlights that over the last 25 years, the meerkat population in the Kalahari has been regulated primarily by variation in annual rainfall and direct density dependence acting through group size, while variation in temperature has played a supporting role. However, with continued temperature rises one of the more certain outcomes for the Kalahari in the coming century, there is the potential for high summer temperatures to have a stronger demographic influence in the near future. Broadly, though our paper goes some way to identifying the specific demographic parameters that are correlated with changes in climate, the emphasis now needs to shift towards understanding the proximate mechanisms that underpin these relationships. This includes examining the role of changes in foraging success, body condition and hormone levels across varying environmental conditions, as well as investigating the extent to which meerkats and other species adjust their behaviour to changes in climate.

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Permits – The long-term data used in this study were collected under permits granted by the ethics committee of the University of Pretoria, South Africa (EC047-16, EC010-13, SOP029-12), and adhered to the standards outlined in the ASAB/ABS guidelines for the Treatment of Animals in Behavioural Research and Training (ASAB, 2012).

Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.br15dvj5> (Thorley et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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